PB87-117479

Plant Architecture and Resource Competition

Utah State Univ., Logan

Prepared for

Corvallis Environmental Research Lab., OR

Oct 86

U.S. Department of Commerce
National Technical Information Service
NTIS

PB87-117479

EPA/600/D-86/244
October 1986

PLANT ARCHITECTURE AND RESOURCE COMPETITION

by

Martyn M. Caldwell
Utah State University
Logan, UT

EPA Grant CR808167

ENVIRONMENTAL RESEARCH LABORATORY
OFFICE OF RESEARCH AND DEVELOPMENT
U.S. ENVIRONMENTAL PROTECTION AGENCY
CORVALLIS, OR 97333

REPRODUCED BY
U.S. DEPARTMENT OF COMMERCE
NATIONAL TECHNICAL
INFORMATION SERVICE
SPRINGFIELD, VA. 22161

TECHNICAL REPORT DATA (Please read Instructions on the reverse before completing)		
1. REPORT NO. EPA/600/D-86/244	2.	3. RECIPIENT'S ACCESSION NO. PB87 117479/AS
4. TITLE AND SUBTITLE Plant architecture and resource competition		5. REPORT DATE October 1986
		6. PERFORMING ORGANIZATION CODE
7. AUTHOR(S) Martyn M. Caldwell		8. PERFORMING ORGANIZATION REPORT NO
9. PERFORMING ORGANIZATION NAME AND ADDRESS Utah State University Logan, Utah		10. PROGRAM ELEMENT NO.
		11. CONTRACT/GRANT NO. CR808167
12. SPONSORING AGENCY NAME AND ADDRESS Environmental Research Laboratory Office of Research and Development U.S.Environmental Protection Agency Corvallis, OR 97333		13. TYPE OF REPORT AND PERIOD COVERED Book Chapter
		14. SPONSORING AGENCY CODE EPA 600/02
15. SUPPLEMENTARY NOTES		

16. ABSTRACT

In a broad sense, successful persistence in a plant community involves not only the immediate competition for resources such as light or soil nitrogen, but also processes such as effective dispersal of propagules and their successful establishment. In the longer term, successful species must also be able to accommodate changes in the environment such as climatic alterations. Although plant structure plays a significant role in phenomena such dispersal, this chapter focuses only on the role of plant architecture in the immediate competition for resources between neighboring plants.

Plant architecture constrains the manner in which plants can develop, apportion and utilize assimilates and also the investment of materials needed to realize growth in height or lateral spread. Thus, it must be an overriding consideration in the manner in which plants compete with one another.

17. KEY WORDS AND DOCUMENT ANALYSIS		
a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group
18. DISTRIBUTION STATEMENT Release to Public	19. SECURITY CLASS (This Report) Unclassified	21. NO. OF PAGES 41
	20. SECURITY CLASS (This page) Unclassified	22. PRICE

EPA Form 2220-1 (9-73)

NOTICE

This document has been reviewed in accordance with U.S. Environmental Protection Agency policy and approved for publication. Mention of trade names or commercial products does not constitute endorsement or recommendation for use.

Plant architecture and resource competition

Martyn M. Caldwell

Utah State University

From: E.-D. Schulze and H. Zwoelfer (eds.) Potentials and Limitations of Ecosystem Analysis. Springer-Verlag, Berlin (1986, in press)

I. Introduction

The character of an ecosystem is determined in part by the balance of competition among higher plant species. In most habitats, the physical environment is conducive to the growth and survival of more species than actually persist and compete at a particular site. Competition is, thus, often a sorting process that determines which plant species occupy a site. The higher plant species composition in turn has a large bearing on species membership in other trophic levels. Though the importance of competition among higher plants is well appreciated and the subject of much study, relatively little progress has been made toward an understanding of how plants compete with one another for resources and which traits are of particular advantage in this competition.

Plant architecture, especially that of woody plants, has received considerable attention from the perspective of developmental patterns and the structure a plant can achieve by virtue of different patterns of bud and shoot development (e.g., Halle et al. 1978, Bell and Tomlinson 1980, Honda et al. 1981, Remphrey and Powell 1984). The emphasis in such work has been on developmental morphology of plants. The relationship between certain structural features of plants and light interception has also been studied (e.g., Horn 1971, Honda and Fisher 1978) but this has usually not been placed in the context of the immediate competition between neighboring plants. Other functional consequences of plant structure such as elastic buckling criteria,

beam loading characteristics, drag and probabilities of uprooting or snapping have been the subject of much research and some elegant theoretical treatment (McMahon and Kronauer 1976, Coutts 1983, Putz et al. 1983). The hydraulic architecture of plants such as the relationship between conducting area of sapwood and leaf area in support of the pipe model theory has also received study (Shinozaki et al. 1964, Waring et al. 1982). Although these functional attributes of plant architecture have important implications for the competitive potential of different species, the direct role of plant architecture in resource competition has received less explicit attention.

The study of competition among higher plants has traditionally centered on the role of competition in structuring ecosystems rather than how plant structure influences competition. The questions traditionally addressed include those of resource and space partitioning in the environment, niche specialization, competitive exclusion and coexistence of species. The dominant theme is often how different species avoid direct resource competition and how this avoidance contributes to niche partitioning. Less commonly considered is the actual process of competition in situations where foliage and root systems of neighboring plants are indeed overlapping and competing for the same resources or space.

Direct investigation of the process of competition in the field is difficult and much of the competition research has dealt with the manifestations of competition rather than the process or mechanisms. The nature and degree of plant competition has been inferred from plant dispersion patterns (whether random, clumped, or evenly spaced), neighborhood analyses (size and spacing relationships among

neighboring plants), the response of plants when neighbors are removed or when root systems are truncated by trenching, or the performance of transplants in new habitats. From such inferential study has arisen a considerable body of experimental literature and theory concerning competition in different habitats (Pielou 1962, Connell 1975, Schoener 1983). This research and theory lie outside the purview of this essay, although aspects of such studies are pertinent to questions of space occupation and resource preemption by neighboring plants.

In a broad sense, successful persistence in a plant community involves not only the immediate competition for resources such as light or soil nitrogen, but also processes such as effective dispersal of propagules and their successful establishment. In the longer term, successful species must also be able to accommodate changes in the environment such as climatic alterations. Although plant structure plays a significant role in phenomena such dispersal, this chapter focuses only on the role of plant architecture in the immediate competition for resources between neighboring plants.

Plant architecture constrains the manner in which plants can develop, apportion and utilize assimilates and also the investment of materials needed to realize growth in height or lateral spread (Watson and Casper 1984, Remphrey and Powell 1984, Maillette 1982). Thus, it must be an overriding consideration in the manner in which plants compete with one another.

II. Traits of a competitive plant

J. P. Grime (1979) has drawn useful generalizations about the characteristics of plant species that he classified as competitors, stress-tolerators and ruderals. His observations of successful

competitors of various growth forms in different environments led him to these general characteristics. Competitive plants should be those than can quickly establish a canopy, either from stored reserve energy or from immediate photosynthesis, and that can achieve both height and lateral spread efficaciously. The competitive advantage stems from the capacity to capture resources quickly by shading competitors above ground and usurping soil moisture and nutrients below ground. Although physiological characteristics such as high photosynthetic rates per unit of foliage material and high nutrient absorption capacities per unit root surface would be of obvious benefit in such a scheme, the link between physiological properties and competitive effectiveness is often less distinct than the relationship between competitiveness and plant structural traits.

A nicely developed example of this comes from a detailed study of shrub and tree species competing for space and light in a hedgerow in central Europe (Kuppers 1984a, b, c, and 1985). Hedgerows between the agricultural fields are composed of several woody species and these progress through a recognizable sequence, or succession, following a periodic cutting which usually occurs at approximately 30- to 40-year intervals. This sequence is largely a result of late successional trees overtopping, and eventually outcompeting the species that first predominate in the early stages of the sequence. The ability to compete in this hedgerow system is not, however, a direct consequence of superior physiological performance of the leaves of the respective species. The early species of this sequence, Rubus corylifolius, Prunus spinosa and Crataegus x macrocarpa actually exhibit 3-fold higher photosynthetic rates per unit leaf area than the tree, Fagus

silvatica, that ultimately dominates in the later stage of succession. Furthermore, when computed on an annual basis, the carbon budgets, i.e., net photosynthesis minus dark respiration, of leaves exposed in the sunlit zones of these hedgerows are also not correlated with competitive ability. Fagus leaves have about 1/3 of the annual carbon gain per leaf area of the earlier, less competitive species. The amount of water transpired per unit photosynthetic carbon gain, an important physiological parameter, also bears no relationship to competitive potential in these later stages of succession.

Since carbon gain potential of the ultimately more competitive species is actually much less than the earlier species, the difference in competitiveness must lie with other properties such as the efficiency with which these species occupy space and develop a canopy that shades competitors. Kuppers (1982, 1985) used several indices to assess the investment required by each of the species to occupy a unit volume of canopy space. The later successional species invest less in carbon and nutrients to occupy canopy volume and also develop a greater leaf density, both of which contribute to a greater capacity to shade competitors. The general allocation pattern of these different species is not so different in that all the species apportion about 10% of their carbon into leaves and all but one species, Rubus, allocate approximately 30% of their carbon to root systems. The differences in canopy development efficiency are primarily a function of the branching patterns and other structural traits which permit the more competitive species to eventually dominate in this system. Although not specifically investigated in this study, competition below ground may have played an important role in addition to the more obvious aboveground space occupation.

The foregoing view of competitive potential focuses on the later stages of succession. Naturally, the earlier successional species have distinct advantages in earlier phases of the hedgerow development and some of these species can elude competition even later in the succession. The early species can grow quickly in the open, sunlit environment of the developing hedge. They also invest heavily in thorns which effectively deter browsing by deer and other herbivores. The late succession species such as Fagus and Acer can, in fact, only develop in the shade of the protective earlier species. A species such as Rubus has vine-like characteristics in that the long, flexible branches may touch the ground and take root allowing the plant to move and explore the more favorable light environments at the edge of the hedgerow. Thus, these relationships are more complicated than simply the competition for light late in succession.

Potential competitiveness cannot be necessarily measured by success or productivity when a species is growing by itself (Donald 1963). This has been vividly demonstrated by trials with various cultivars of crop and pasture species in which there was no positive relationship between growth or yield of cultivars of a species in monoculture and the ability of these cultivars to compete and be productive in mixtures with other species (Eagles 1983). Sometimes, the relationships are even inverse in that productivity of cultivars in monoculture has been shown to be inversely proportional to their competitive effectiveness in mixtures (Sakai and Gotoh 1955, Jennings and Jesus 1968). Winning a competition for light and other resources may often involve subtle differences between species as will be illustrated in some subsequent examples in this essay.

III. Competition for light

The interspecific competition among plants to intercept sunlight is observable and, thus, tractable for study. Nevertheless, research has focused more on the outcome of light competition rather than the process. Leaves, by virtue of their planar shape and optical properties, are very effective shading objects. Less than 5% of the solar radiation in the 400-700 nm waveband, which drives photosynthesis, is transmitted by most leaves (Gates 1980). Therefore, most of the radiation, whether in monoculture or in mixed-species systems, is absorbed in the uppermost part of the canopy. Despite the geometrical complexity of canopies with leaves and stems oriented at different angles and the resulting gaps between foliage elements, absorption of sunlight follows a logarithmic extinction pattern much like radiation extinction in a more homogeneous optical medium such as water (Figure 1). Thus, competitive advantage can accrue quickly by slight height advantages that place one species' uppermost foliage elements above those of another species. Simple overtopping of one species by another due to height differences leads to predictable consequences in the competiton for light. For example, suppression of western hemlock (Tsuga heterophylla) by Douglas-fir (Pseudotsuga menziesii) in even-aged, second-growth mixtures is a clear case of height advantage of Pseudotsuga and the resulting shading of Tsuga crowns (Wierman and Oliver 1979). Even in monocultures, differences in individual plant competitiveness can be reasonably well explained by differences in individual plant height which then result in more pronounced changes in plant size with respect to neighboring plants (Ford and Diggle 1981, Benjamin 1984). Although overtopping is a

straightforward example of light competition, this situation can be much more complicated if height differences are subtle and foliage of competing plants is represented throughout several strata of the stand. At different layers, leaves of a plant are being shaded and are shading leaves of the same individual as well those of neighboring plants. Furthermore, these relationships can change quickly through time.

The subtleties of competitive advantage are best manifested in experiments in which the competitors are closely related species since small differences in plant structure, timing and physiological attributes can be expressed. Harper and Clatworthy (1963) studied two species of Trifolium that are so similar they are difficult to distinguish from one another in vegetative phases of growth. In early stages of development, T. repens, through germinating from smaller seed and having smaller cotyledons than T. fragiferum, still managed to achieve faster rates of true leaf production and develop more photosynthesizing leaf surface in the first 12 weeks (Figure 2). In mixtures, T. repens also benefited by having longer hypocotyls that were also more responsive to shading and elongated more effectively than those of T. fragiferum. At 15 weeks, as shown in Figures 2 and 3, the two species were very comparable in monoculture, and light extinction profiles in both monocultures and the mixture were very similar. However, T. repens was at apparent advantage in the mixture. In subsequent weeks, although T. fragiferum in monoculture exhibited more than twice as much growth as T. repens as a consequence of their natural growth periodicities, T. repens in mixture with T. fragiferum still maintained an equivalent growth and leaf area

production to that of T. fragiferum. The exact reasons for the competitive ability of T. repens, especially in the later stages of the experiment when its monoculture performance was inferior, are not clear and may have involved not only complexities of light competition, but also belowground interactions. Had the experiment run still longer, the competitive advantage might have shifted in favor of either species. Furthermore, factors such as resistance to lodging in periods of heavy wind or precipitation, or the alteration of the canopy by grazing could shift the balance of competition in different directions at any stage of the sequence following sowing.

A very similar experiment was conducted by Williams (1963) with three annual species of Trifolium grown in monoculture and in paired mixtures. As in the study of Harper and Clatworthy (1963), early advantage by virtue of greater cotyledon area did not result in a continued advantage throughout the experiment. Also, the species most efficient in light interception and net assimilation rates in monoculture was actually intercepting the least amount of light in mixtures. The importance of leaf positioning by virtue of petiole characteristics was apparent in this study as location of leaves high in the canopy appeared to explain much of the difference in competitive ability.

On a theoretical basis, not only height of the foliage but also foliage inclination angles should be important in light competition. For monocultures, the most efficient array of foliage inclination angles for total canopy light harvesting is a progressive shift from steeply inclined foliage at the top of the canopy to more horizontal foliage elements near the bottom (e.g., Rhodes and Stern 1978). This allows for better penetration of sunlight into the stand and more

efficient photosynthetic light harvesting. Quite the opposite should be the case for effectiveness in light competition. For plants of similar height, those which intercept more light at the top of the canopy with more horizontally oriented foliage will be more effective in shading neighbors. In this context, solar tracking leaves, i.e., those that maintain an angle close to perpendicular with the solar beam should be the most effective in competition for light. Although the ecological implications of solar tracking have been explored in detail for isolated plants (e.g., Ehleringer and Forseth 1980), the significance of solar tracking for light competition in closed canopies has received little attention. For that matter, the general application of light penetration theory to questions of competition has not been well exploited.

Beginning with the pioneering work of Monsi and Saeki (1953), efforts to produce theoretical descriptions and predictions of light penetration in canopies have enjoyed considerable success. This body of theory, based largely on gap probabilities, serves well to describe both direct beam and diffuse radiation penetration in plant canopies. Such theory would seem to be readily extendable to questions of light competition. Yet, there are few examples where this has been implemented. Rimmington (1984) extended the very basic light extinction equations of Saeki (1963), which describe the transmission of light downward through a layer of vegetation for a single species, to light interception and photosynthesis by two species in mixture. The model can accommodate different proportions of foliage of the two species in different horizontal layers and the light extinction characteristics of both species. The model does not have many of the

optical refinements of some other models of light extinction that account for reflected radiation in different directions and that compute direct beam and diffuse components separately. Nevertheless, it adequately described the outcome of light competition for experiments with Trifolium repens and Lolium perenne.

An even simpler approach to calculation of light competition was taken by Ford and Diggle (1981) in planted monocultures. Rather than using gap probability theory, they simply defined an angle describing a cone of shading influence that taller plants exert over shorter plants. Shorter plants have no influence on taller plants; thus, this competition is distinctly one sided. However, a short plant may be suppressed by overlapping shading influence cones of more than one neighbor. They reported that this modelling approach worked quite adequately for describing plant size distributions resulting from intraspecific competition in monocultures.

Highly complex and detailed models of light penetration and reflection in plant canopies have been developed. An example of a particularly comprehensive and refined model is that of Norman et al. (1985) which has been developed for remote sensing applications. (When viewed from above the canopy, there are complex optical signals that result not only from the reflection of individual leaves, but also from the movement of diffuse radiation downward and upward among different foliage elements. There are also spectral modifications resulting from the location of foliage elements of different species in the canopy. All of this is dependent on the angle of the sun with respect to the canopy and also the angle of the observer). Although this model has been developed for remote sensing applications, such a comprehensive numerical analysis might serve well in assessing the

more subtle aspects of light competition in mixed-species stands where obvious overtopping of one species by another does not explain the competitive process.

IV. Morphological flexibility and the light environment

In the competition for light, plants are balancing their investment in leaves, which are the prime photosynthetic and shading organs, and supporting structures such as stems and petioles that place the leaves in the most advantageous position for competition. Height growth is of prime importance when light competition is present and leaf production is most important when a plant is in a position to intercept light. If a plant can perceive the immediate light environment and accordingly alter the allocation of growth to stems or leaves, this would be of obvious advantage in communities where added height growth would put the plant at advantage with respect to competitors. Many species do, in fact, exhibit such a flexibility in response to the light environment. This is, however, primarily a response to the spectral composition of the light rather than a response to the intensity. Figure 4 illustrates a classical example of this for Chenopodium album. The plants shown were exposed to the same intensity of visible light, but to different ratios of red and far-red light (far-red being the region of the spectrum just beyond 700 nm). The plant receiving the far-red enriched light exhibited the increased internode elongation and reduced branching and leaf production. Sunlight filtered through the green foliage of a canopy is relatively far-red rich since green leaves absorb strongly at wavelengths shorter than 700 nm, but transmit and reflect predominately at wavelengths longer than 700 nm (Holmes and Smith 1977). The response illustrated

here would be of obvious benefit to alter the balance between height and foliage production as a plant experiences different degrees of shading.

The control of these allocation shifts has been clearly shown to be mediated by the phytochrome pigment which has two forms that absorb strongly in the red and far-red parts of the spectrum. This pigment is in essence measuring light ratios and in cases such as this is an excellent detector of shade from living foliage, to a large extent irrespective of absolute light intensities (Holmes 1983).

Plant species, however, vary considerably in this flexibility of allocation in response to light. It does not appear to be a phenomenon of herbaceous shade-tolerant forest floor species where increased stem elongation at the expense of leaf production would only be detrimental. Such plants would never have the prospect of growing above the overhead tree canopy and would simply sacrifice their limited energy to production of a tall and spindly plant with little leaf area. Thus, one might expect that species most able to tolerate shade by the capacity to photosynthesize efficiently under low light conditions, would be those least responsive in their growth allocation when in red or far-red light. When the allocation flexibility has been examined for species from different habitats, indeed a general inverse relationship between shade tolerance and responsiveness to red/far-red ratios has been found (Figure 5).

Study of this allocation flexibility has been limited almost entirely to herbaceous plant species, although one study with Pinus radiata did indicate that this tree also exhibits a similar response to red/far-red light ratios (Morgan et al. 1983).

Apart from a simple elongation or height growth response to spectral changes in the red or far-red, plants may also adjust branching patterns and growth direction. At this juncture, this can only be offered as a hypothesis since I am not aware of experimental evidence to support this notion. Returning to the hedgerow work of Kuppers discussed earlier, a single tree growing in the dense hedgerow can occupy a very contorted space in this tightly packed assemblage of trees and shrubs (Figure 6). The growth form and branching pattern is obviously very much altered from that of a free-standing tree. Yet, Kuppers reports (personal communication) that the canopies of these shrubs and trees and hedgerow seldom overlapped in an interdigitating manner. Thus, the extent and direction of branch growth apparently respond to the presence of neighboring branches. Whether interdigitation of neighboring branches is prevented by an avoidance growth response or whether these branches do initially grow into the neighbor's canopy and subsequently die back is not clear, since the growth interaction between neighboring canopies was not a major thrust of this work. If an avoidance growth response does exist in this example or in other situations, it could be mediated by a response to zones of far-red rich light as would be found within the canopy of a neighboring plant.

Alternatively, the lack of overlap among canopies may be the result of abrasion of buds and growing tips as wind causes movement of the vegetation. This has, for example, been suggested as the cause of distinct intervals between the outer elements of mangrove tree canopies (Putz et al. 1984). The size of the "crown shyness" gaps between the tree canopies portrayed in Figure 7 was correlated with the degree to which individual trees swayed in the wind. They also

observed broken twigs and fewer leaves on branches bordering the crown shyness gaps, although a systematic study of twig development and abrasion was not undertaken. They could not rule out the role played by shading or other alterations of the light environment. Wind shearing of peripheral branches has also been reported in other forest systems (Halle et al. 1978).

Whatever the causes may be, the altered architecture of plants growing in close association with one another has an undeniable bearing on the dynamics of light competition. It is surprising that this has not received more study.

Structural flexibility in placement of individual foliage elements in the canopy space may also have important implications for competitive effectiveness. There is an obvious advantage in positioning a large proportion of the foliage at upper levels of a canopy. However, even in lower levels of the canopy, if leaves can be placed in favorable microsites, light interception will be improved. This could be of particular importance for species whose basic growth form precludes overtopping of other species. Indirect evidence indicates this to be the case for white clover (Trifolium repens) (Boller and Nosberger 1985). They conducted a detailed study of canopy architecture and photosynthetic activity of leaves of different age and canopy position in which individual leaf photosynthesis was measured in the canopy and compared with leaf photosynthetic activity under defined light conditions. In the intact stand, the younger leaves exhibited substantially greater photosynthetic rates than older leaves at the same height in the canopy even though photosynthetic measurements of individual leaves removed from the stand under defined

light conditions indicated no pronounced effect of leaf age on photosynthesis. They concluded that the unexpectedly greater photosynthetic rates of younger leaves in the intact canopy measurements indicted that as young leaves were unfolded at different heights in the canopy, they were being located in more favorable light microsites. Although they could not directly assess the individual leaf light environments, their results do indicate a nonrandom location of younger leaves in the canopy. Whether this was by a phototropic or red/far-red light response to small sunflecks, or still some other mechanism, is not known.

Competition for light may involve many rather subtle foliage positioning phenomena and much of this depends on the morphological flexibility of the plant and a manner of sensing the light environment. While mechanistic and quantitative study of these phenomena in the context of light competition is tractable, it is not a trivial problem.

V. Competition below ground

The process of light competition, though complicated, is readily envisaged since one can see how foliage elements shade one another. How plants compete belowground is much less discernible and has received comparatively little study. Even questions such as how much root systems of neighboring plants interdigitate and overlap have been little addressed. As I have recently completed an essay on root system competition (Caldwell 1986), which specifically addresses information that can be brought to bear on such questions, this section of the present essay is necessarily very brief.

Belowground plant architecture has been described for both

diffuse root systems (e.g., Kutschera and Lichtenegger 1982, Fitter 1982) and for larger roots and rhizomes (Bell and Tomlinson 1980, Antos and Zobel 1984, Putz et al. 1983). These studies approach root architecture from the standpoint of developmental patterns, root element longevity, branching orders, and root replication units. Direct relationships between root structural characteristics and competitive effectiveness is largely limited to circumstantial evidence, such as correlations between root structural features and success in competition (Steffens 1984), or theoretical treatments of root morphological parameters that should increase competitive potential (Baldwin et al. 1972, Baldwin 1976, Caldwell and Richards 1986, Caldwell 1986). Understanding the nature of root competition is another matter.

Although the information is scant, root systems of neighboring plants may frequently intermingle and several experiments indicate quite clearly that belowground competition can be quite pronounced. Even in situations where plant shoot systems are tightly packed and clearly are competing for light, root competition can be even more pronounced than shoot competition as has been demonstrated by numerous experiments in which root and shoot systems were separately partitioned (e.g., Martin and Field 1984, Cook and Ratcliff 1985).

Whether individual roots are depleting soil resources to levels not accessible to roots of competitors, or whether competition is more a matter of soil space occupation by an aggregate of roots of one plant to at least the partial exclusion of roots of its neighbors, is not known. The exact location of roots in the soil space is critical to an understanding of such questions. The uptake of soil moisture and

mineral nutrients, especially those of low diffusion capacity in soil, can often be more limited by diffusion resistance in the soil rather than in their movement into the root itself. Thus, the distance and pathway of movement in the soil, and therefore the location and arrangement of active root elements, is a primary consideration.

Study of the distribution of root elements on a small scale as it relates to competition for soil nutrients has been seldom undertaken. Fusseder (1985) recently reported such a study on root distribution of maize in a planted field in relation to expected zones of mineral nutrient absorption by individual roots. Radioactive markers were used to trace individual root locations for plants in adjacent rows. At the time of sampling, there appeared to be very little direct competition for macronutrients between adjacent rows of plants, since only a small percentage of the neighboring plants roots were close enough to influence nutrient uptake of one another. Although this view of competition is limited to a consideration of the immediate competition for resources at the time of sampling and cannot account for processes such as resource or space preemption through root growth, it does provide useful insight into the nature and location of root interactions. There do not appear to be similar reports of such studies with species mixtures.

At a coarser scale of resolution, an analogous study involving species mixtures was conducted by Bookman and Mack (1982). Using a double isotope labeling they followed the distribution of roots of a pair of competing grasses planted in pots. They did not determine the positions of individual roots as in the Fusseder study, but instead simply determined the presence or absence of roots of the two species in different parcels of soil within the pot. By staggering the

planting time of the annual grass, Bromus tectorum, among previously planted perennial grass seedlings of Poa pratensis, they demonstrated a distinct tendency of the roots of the annual grass to be excluded from different soil parcels by the previously established roots of the perennial grass. The nature or reason for this exclusion is not known, but the phenomenon is of obvious pertinence in understanding belowground competition.

Even on the scale of whole root systems, a demonstration of where different species are acquiring soil resources in mixed species systems is difficult and there are few examples of experiments addressing this in the field. The exploitation of soil resources at different depths has been inferred from mappings of root systems (e.g. Yeaton et al. 1977, Kummerow et al. 1977) and the tendency of different species from a community to develop roots at different soil depths when planted in isolation (Parrish and Bazzaz 1976). The coexistence of species with different rooting depths has also been treated theoretically and in controlled experiments to test this theory (Berendse 1979, 1981, 1982). However, there are few reports of direct measurements of the location of resource acquisition in species mixtures under field conditions. One such direct determination of phosphate uptake in mixtures of Trifolium repens and Lolium perenne (Fig. 8) shows clearly that the location of resource uptake can be very different in species mixtures than when species are grown in monoculture. These experiments were conducted in a series of separate plots in which ^{32}P isotope was placed at different depths in each plot. The composite behavior is then represented in Figure 8. There was a pronounced downward shift in maximum depth of phosphate uptake

by the Lolium when in mixture with clover. Whether there were also changes in the root distributions with depth in the mixed plots, or whether these displacements in phosphate uptake patterns were simply the result of competition, is not known since root distributions were not mapped in this work.

VI. Concluding remarks

A melding of information on plant structural features, the sites and timing of resource acquisition and how these relate to competitive advantage or disadvantage is not a trivial undertaking. Even posing tractable hypotheses and experimental designs on questions of resource acquisition in competition is difficult. Yet, the availability of better experimental tools and more refined theory of processes such as light interception in canopies and nutrient uptake below ground, are becoming available to address such questions.

Much is known about the developmental morphology of plants, at least above ground, and the structural flexibility that different species innately posses. However, less is known about how this morphological development responds to specific environmental cues; the elongation response to red/far-red light ratios is a notable exception. An understanding of such specific environmental cue responses would contribute greatly to our understanding of the process of competition for aboveground space and light and which species may have advantage under certain circumstances.

Below ground this understanding is much more rudimentary. Even simple questions of root system overlap and the distribution of root systems in different soil environments have been little explored. Although the structural features of root systems may well be more

important than many root physiological characteristics in competitive effectiveness, this can only be surmised at the present time by theoretical models and these models take a very simplifed approach to root system structure.

Figure Legends

Figure 1. Extinction of solar radiation in a canopy of Quercus coccifera as a function of depth in the canopy (expressed as accumulated leaf area index), dashed line (Meister and Caldwell, unpublished) and extinction of light in water, a more optically homogeneous medium, solid line (after Talling 1970).

Figure 2. The course of total leaf area of stands of two clover species in monoculture and in mixtures (redrawn from Harper and Clatworthy 1963).

Figure 3. Vertical distribution of leaf area and light extinction profiles of two clover species in monoculture and mixture 15 weeks after sowing (adapted from Harper and Clatworthy 1963).

Figure 4. Chenopodium album seedlings grown at the same total quantum flux (100 umoles $\cdot m^{-2} \cdot s^{-1}$, 400-700 nm) but under different ratios of of far-red and red radiation. The plant on the right received a high ratio of far-red to red and the plant on the left a low ratio. (drawn from a photograph in Morgan and Smith 1976.)

Figure 5. Internode extention response of species differing in shade tolerance as a function of the proportion of red and far-red radiation under which the plants were grown. The total quantum flux density

(400-700 nm) was the same (adapted from Holmes 1983).

Figure 6. Growth form of Crataegus trees in isolation (above), or in a hedgerow (below) in competition with canopies of other species (indicated by grey areas) (adapted from Kuppers 1982).

Figure 7. Upward view of crowns of Avicennia germinans during calm conditions illustrating gaps between the outer perimeters of individual tree crowns (above) and a correlation of the size of gaps between tree crowns and the displacement, or sway of individual trees under windy conditions (below) (redrawn from Putz et al. 1984).

Figure 8. Phosphate uptake by monocultures and mixtures of Trifolium repens and Lolium perenne as a function of soil depth. (adapted from Goodman and Collison 1982).

Acknowledgements

Some of the information and concepts contained in this essay resulted from research supported by the U.S. National Science Foundation (DEB 8207171), the Environmental Protection Agency (CR 808167), and the Utah Agricultural Experiment Station. Comments by P. Barnes and S. Flint and drafting of figures by C. Warner are gratefully appreciated.

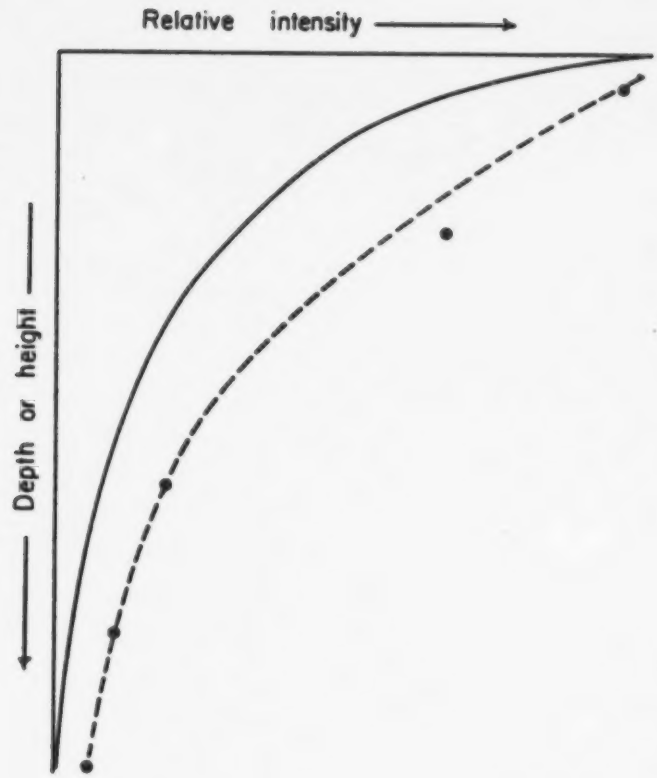

Figure 1.

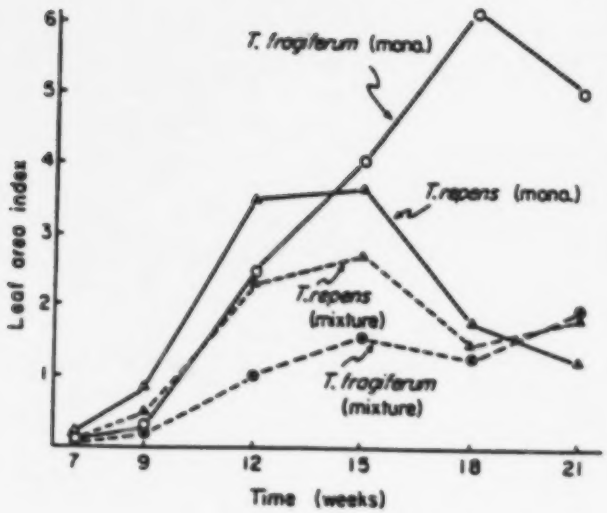

Figure 2.

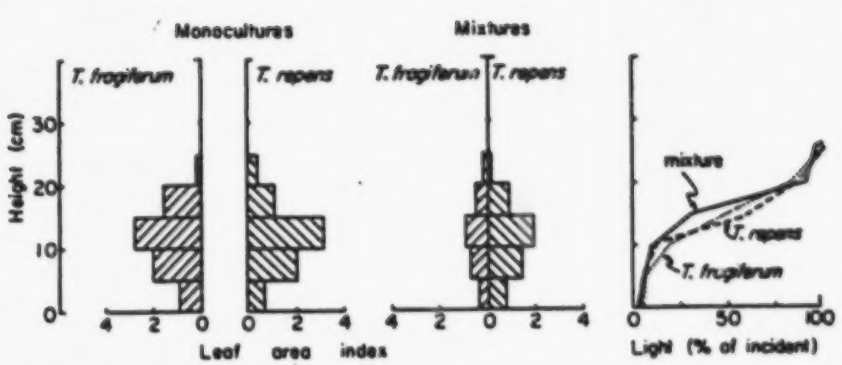

Figure 3.

Figure 4.

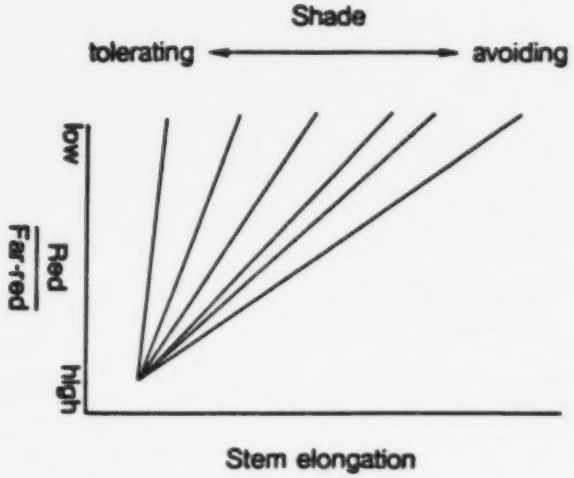

Figure 5.

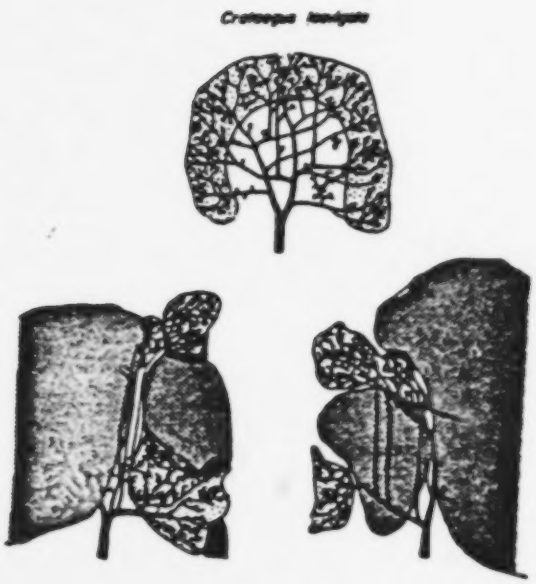

Figure 6.

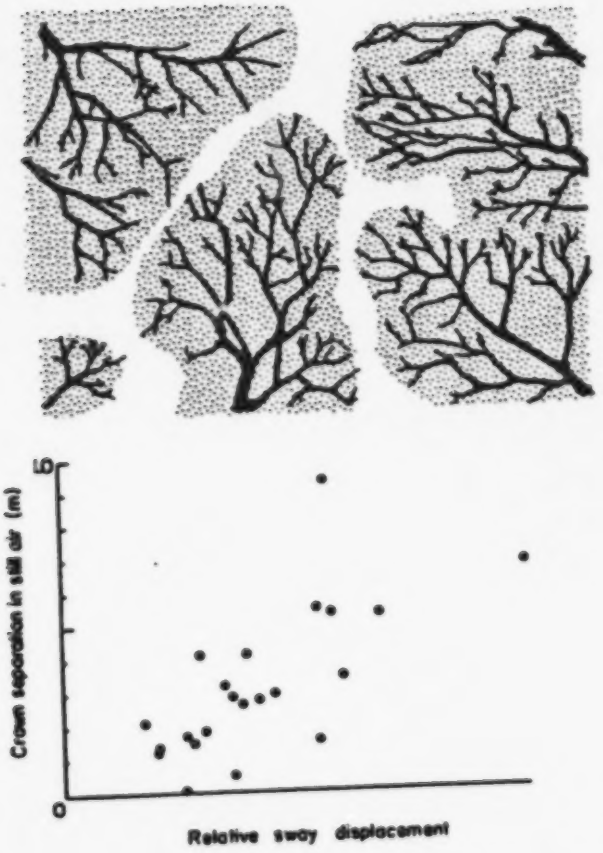
5
0
Crown separation in still air (m)
Relative sway displacement

Figure 7.

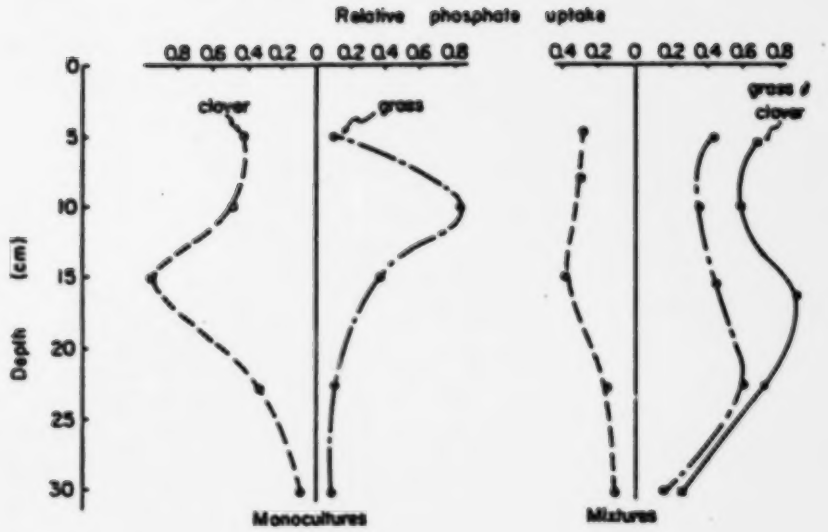
Relative phosphate uptake
0.8 0.6 0.4 0.2 0 0.2 0.4 0.6 0.8
0.4 0.2 0 0.2 0.4 0.6 0.8
Depth (cm)
0
5
10
15
20
25
30
clover
grass
Monocultures
grass +
clover
Mixtures

Figure 8.

References

Antos, J. A. and D. B. Zobel. 1984. Ecological implications of belowground morphology of nine coniferous forest herbs. Bot. Gaz. 145:508-517.

Baldwin, J. P. 1976. Competition for plant nutrients in soil; a theoretical approach. J. Agric. Sci., Camb. 87:341-356.

Baldwin, J. P., P. B. Tinker and P. H. Nye. 1972. Uptake of solutes by multiple root systems from soil. II. The theoretical effects of rooting density and pattern on uptake of nutrients from soil. Plant Soil 36:693-708.

Bell, A. D. and P. B. Tomlinson. 1980. Adaptive architecture in rhizomatous plants. Bot. J. Linnean Soc. 80:125-160.

Benjamin, L. R. 1984. Role of foliage habit in the competition between differently sized plants in carrot crops. Ann. Bot. 53:549-557.

Berendse, F. 1979. Competition between plant populations with different rooting depths I. Theoretical considerations. Oecologia 43:19-26.

Berendse, F. 1981. Competition between plant populations with different rooting depths II. Pot experiments. Oecologia 48:334-341.

Berendse, F. 1982. Competition between plant populations with different rooting depths III. Field experiments. Oecologia 53:50-55.

Bookman, P. A. and R. N. Mack. 1982. Root interaction between Bromus tectorum and Poa pratensis: a three-dimensional analysis. Ecology 63:640-646.

Boller, B. C., and J. Nosberger. 1985. Photosynthesis of white clover leaves as influenced by canopy position, leaf age, and temperature. Ann. Bot. 56:19-27.

Caldwell, M. M. 1986. Root system competition in natural communities. in P. J. Gregory (ed.) Root development and function. Effects of the physical environment. Cambridge Univ. Press (in press).

Caldwell, M. M. and J. H. Richards. 1986. Competing root systems: Morphology and models of root absorption. in T. Givnish (ed.) On the economy of form and function. Cambridge Univ. Press (in press).

Connell, 1975. Producing structure in natural communities. in M. L. Cody and J. M. Diamond, eds. Ecology and evolution of communities. Belknap. Cambridge, Mass. p. 460-490.

Cook, S. J. and D. Ratcliff. 1985. Effect of fertilizer, root and shoot competition on the growth of siratro (Macroptilium atropurpureum) and green panic (Panicum maximum var. trichoglume) seedings in a native speargrass (Heteropogon contortus) sward. Austrl. J. Agric. Res. 36:233-245.

Coutts, M. P. 1983. Root architecture and tree stability. Plant Soil 71:171-188.

Donald, C. M. 1963. Competition among crop and pasture plants. Advan. Agron. 15:1-118.

Eagles, C. F. 1983. Relationship between competitive ability and yielding ability in mixtures and monocultures of populations of Dactylis glomerata L. Grass Forage Sci. 38:21-24.

Ehleringer, J. and I. Forseth. 1980. Solar tracking by plants. Science 210:1094-1098.

Fitter, A. H. 1982. Morphometric analysis of root systems: application of the technique and influence of soil fertility on root system development in two herbaceous species. Plant Cell Environ. 5:313-322.

Eord, E. D. and P. J. Diggle. 1981. Competition for light in a plant monoculture modelled as a spatial stochastic process. Ann. Bot. 48:481-500.

Fusseder, A. 1985. Verteilung des Wurzelsystems von Mais im Hinblick auf die Konkurrenz um Makronahrstoffe. Z. Pflanzenernaehr. Bodenk. 148:321-334.

Gates, D. M. 1980. Biophysical ecology. Springer-Verlag, New York. 611 p.

Goodman, P. J. and M. Collison. 1982. Varietal differences in uptake of ^{32}P labelled phosphate in clover plus ryegrass swards and monocultures. Ann. Appl. Biol. 100:559-565.

Grime, J. P. 1979. Plant strategies and vegetation processes. Wiley, New York. 222 pp.

Halle, F., R. A. A. Oldeman, P. B. Tomlinson. 1978. Tropical trees and forests: An architectural analysis. Springer-Verlag, New York. 441 pp.

Harper, J. L. and J. N. Clatworthy. 1963. The competitive biology of closely related species VI. Analysis of the growth of Trifolium repens and T. fragiferum in pure and mixed populations. J. Exp. Bot. 14:172-190.

Holmes, M. G. and H. Smith. 1977. The function of phytochrome in the natural environment--II. The influence of vegetation canopies on the spectral energy distribution of natural daylight. Photochem. Photobiol. 25:539-545.

Holmes, M. G. 1983. Perception of shade. Phil. Trans. R. Soc. Lond. B 303:503-521.

Honda, H., and J. B. Fisher. 1978. Tree branch angle: Maximizing effective leaf area. Science 199:888-890.

Honda, H., P. B. Tomlinson, and J. B. Fisher. 1981. Computer simulation of branch interaction and regulation by unequal flow rates in botanical trees. Amer. J. Bot. 68:569-585.

Horn, 1971. The adaptive geometry of trees. Princeton Univ. Press, Princeton, N. J. 144 p.

Jennings, P. R. and Jesus, J. de 1968. Studies on competition in rice. 1. Competition in mixtures of varieties. Evolution 22:119-124.

Kummerow, J., D. Krause and W. Jow. 1977. Root systems of chapparral shrubs. Oecologia 29:163-177.

Kuppers, M. 1982. Kohlenstoffhaushalt, Wasserhaushalt, Wachstum und Wuchsform von Holzgewachsen im Konkurrenzgefuge eines Heckenstandortes. Dr. Thesis, Bayreuth

Kuppers, M. 1984a. Carbon relations and competition between woody species in a Central European hedgerow. I. Photosynthetic characteristics. Oecologia 64:332-343.

Kuppers, M. 1984b. Carbon relations and competition between woody species in a Central European hedgerow. II. Stomatal responses, water use, and hydraulic conductivity in the root/leaf pathway. Oecologia 64:344-354.

Kuppers, M. 1984c. Carbon relations and competition between woody species in a Central European hedgerow. III. Carbon and water balance on the leaf level. Oecologia 65:94-100.

Kuppers, M. 1985. Carbon relations and competition between woody species in a Central European hedgerow. IV. Growth form and partitioning. Oecologia 66:343-352.

Kutschera, L. and E. Lichtenegger. 1982. Wurzelatlas mitteleuropaeischer Gruendlandpflanzen. B. I. Monocotyledoneae, 516 pp. Stuttgurt: Gustav Fischer, Stuttgart.

Maillette, L. 1982. Structural dynamics of silver birch I. The fates of buds. J. Appl. Ecol. 19:203-218.

Martin, M. P. L. D. and R. J. Field. 1984. The nature of competition between perennial ryegrass and white clover. Grass Forage Sci. 39:247-253.

McMahon, T. A. and R. E. Kronauer. 1976. Tree structures: Deducing the principle of mechanical design. J. Theor. Biol. 59:443-466.

Monsi, M. and T. Saeki. 1953. Uber den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung fur die Stoffproduktion. Jap. J. Bot. 14:22-52.

Morgan, D. C., H. Smith. 1976. Linear relationship between phytochrome photoequilibrium and growth in plants under simulated natural radiation. Nature 262:210-212.

Morgan, D. C., D. A. Rook, I. J. Warrington, and H. L. Turnbull. 1983. Growth and development of Pinus radiata D. Don: the effect of light quality. Plant, Cell Environ. 6:691-701.

Norman, J. M., J. M. Welles and E. A. Walter. 1985. Contrasts among bidirectional reflectance of leaves, canopies, and soils. I.E.E.E. Trans. Geosci. Remote Sensing. GE-23:659-667.

Parrish, J. A. D. and F. A. Bazzaz. 1976. Underground niche separation in successional plants. Ecology 57:1281-1288.

Pielou, E. C. 1962. The use of plant-to-neighbor distances for detection of competition. J. Ecol. 50:357-367.

Putz, F. E., P. D. Coley, K. Lu, A. Montalvo and A. Aiello. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. Can. J. For. Res. 13:1011-1020.

Putz, F. E., G. G. Parker and R. M. Archibald. 1984. Mechanical abrasion and intercrown spacing. Amer. Midl. Nat. 112:24-28.

Remphrey, W. R. and G. R. Powell. 1984. Crown architecture of Larix laricina saplings: shoot preformation and neoformation and their relationships to shoot vigour. Can. J. Bot. 62:2181-2192.

Rhodes, I. and W. R. Stern. 1978. The physiological basis for variation in the yield of grass/clover mixtures. in C. E. Wright (ed.) Plant physiology and herbage production. British Grasslands Society, Hurley. p. 175-189.

Rimmington, G. M. 1984. A model of the effect of interspecies competition for light on dry-matter production. Austrl. J. Plant Physiol. 11:277-286.

Saeki, T. 1963. Light relations in plant communities. in L. T. Evans (ed.) Environmental control of plant growth. Academic Press, New York. p. 79-94.

Sakai, K. I. and K. Gotoh. 1955. Studies on competition in plants. IV. Competitive ability of F_1 hybrids in barley. J. Heredity 46:139-143.

Schoener, T. W. 1983. Field experiments on interspecific competition. Amer. Nat. 122:240-285.

Shinozaki, K., K. Yoda, K. Hozumi and T. Kira. 1964. A quantitative analysis of plant form--The pipe model theory. I. Basic analyses. Jap. J. Ecol. 14:97-105.

Steffens, D. 1984. Wurzelstudien und Phosphat-Aufnahme von Weidelgras und Rotklee unter Feldbedingungen. Z. Pflanzenernaehr. Bodenk, 147:85-97.

Talling, J. F. 1970. Generalized and specialized features of phytoplankton as a form of photosynthetic cover. in Prediction and measurement of photosynthetic productivity. Centre Agric. Publ. Wageningen, The Netherlands. p. 431-445.

Waring, R. H., P. E. Schroeder and R. Oren. 1982. Application of the pipe model theory to predict canopy leaf area. J. For. Res. 12:556-560.

Watson, M. A. and B. B. Casper. 1984. Morphogenetic constraints on patterns of carbon distribution in plants. Ann. Rev. Ecol. Sys. 15:233-258.

Wierman, C. A. and C. D. Oliver. 1979. Crown stratification by species in even-aged mixed stands of Douglas-fir - western hemlock. Can. J. For. Res. 9:1-9.

Williams, W. A. 1963. Competition for light between annual species of Trifolium during the vegetative phase. Ecology 44:475-485.

Yeaton, R. I., J. Travis and E. Gilinsky. 1977. Competition and spacing in plant communities: the Arizona upland association. J. Ecol. 65:587-595.